ROLE OF BORON IN PLANT GROWTH: A REVIEW

Waqar Ahmad*, A. Niaz**, S. Kanwal, Rahmatullah*** and M. Khalid Rasheed****

ABSTRACT

Boron (B) is considered as an essential element for plant growth and development. Sexual reproduction in plant is more sensitive to low B, than vegetative growth. Considerable research activities have been directed at accentuating the physiological and biochemical role of B in plant growth and development. This paper reviews the literature (upto the year 2006) focusing on the role of boron in cell wall integrity, cell division, plasma membranes, phenol metabolism, and its requirement for the nitrogen fixation and in the reproductive growth of plants.

KEYWORDS: Boron; plant growth; cell division; cell wall; Pakistan.

INTRODUCTION

Mineral nutrition of plants is important for controlling physiological and biochemical processes of plants. Its deficiency may lead to changes in these processes and disturbed plant growth and yield. Boron is one of mineral nutrients that are required for normal plant growth. The essentiality of B for growth and development of higher plants has been earlier demonstrated (27, 43, 46). The main functions of boron relate to cell wall strength and development, cell division, fruit and seed development, sugar transport and hormone development. Some functions of boron interrelate with those of nitrogen, phosphorus, potassium and calcium in plant. The most important functions of boron in plants are thought to be its structural role in cell wall development; and stimulation or inhibition of specific metabolism pathways.

Boron and plant cell wall

Plant cell wall is composed of three main layers i.e. primary wall, secondary wall and middle lamella. Primary wall is set down by cells before and during active growth and comprises pectic polysaccharides (Ca. 30%), cross-linking

***Sustainable Land Management Project, Ministry of Environment, Islamabad Email: waqqar80@gmail.com, **Soil Chemistry Section, AARI, Faisalabad, ***Plant Nutrition Lab., Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad, Pakistan.**

glycans-hemicellulose (Ca. 25%), cellulose (15-30%) and protein (Ca. 20%) (13). Secondary wall in some cells deposits additional layers inside the primary wall. This occurs after growth stops or when the cell begins to differentiate. The secondary wall is mainly for support and comprises primarily cellulose and lignin. Middle lamella that binds adjacent cells is composed of pectic polysaccharides. The actual content of wall components varies with species and age. Some researchers estimate that over 90 percent of total B is localized in cell walls (26, 29). Boron along with Ca^{++} is able to form complexes with several cell wall components such as pectins (21), polyhydroxyl polymers, polyols and Ca^{++} (31, 44). This is the reason that B is implicated in synthesis and stability of cell wall (16) by forming esters with cis diol groups present in cell wall (26). This provides rigidity, strength and shape to the cell.

Cell division

Boron is considered to be essential for actively growing regions of plants, such as root tips, new leaf and bud development. According to Rerkasem (37) boron is especially required more in meristematic cells than in mature tissues. That is why; first effect of boron deficiency usually appears in meristems, as described by Warington (46). Higher meristematic B requirement may rise because of low phloem transport from shoots to other parts of plant, leading to higher accumulation of B in leaves (37).

Ion fluxes

Boron plays an important role in both structural and functional integrity of plasma membranes (28, 31). In B-deficient plants, plasma membranes are highly leaky and lose their functional integrity (11). In many instances, it is proved that fleet alterations in ion fluxes i.e. H^+, K^+, Rb^+, PO_4^{-3}, and Ca^{+2} is associated with B deficiency (38, 39).

The proton efflux by membrane-bound ATPases is a main driving force for ion uptake and responsible for a gradient in electrical potential across the membranes (36, 41). The stimulated activity of plasma membrane NADH oxidase and H^+ secretion in cultured carrot cells with boron has also been reported by Barr and Crane (3). Apparently, auxin affects B-induced H+ extrusion. According to Hu and Brown (20) the stimulatory effect of B on H^+-ATPase activity requires the presence of auxin, or enhancement in proton release by auxin requires the presence of B. In the studies with sunflower root cells and dense leaved elodea (*Elodea densa*) leaf cells, a significant depolarisation of membranes was found after transfer of cells from Bcontaining to B-free solution. Hence, boron nutrition has marked effects on proton secretion and creation of an electrical potential gradient across the membranes (5).

Boron supply enhances the activity of membrane bound ATPase and subsequently causes hyperpolarization of plasma membrane by stimulating K^+ ion uptake The pumping activity of the membranes with subsequent membrane hyperpolarization, results in an increased driving force for K^+ influx (42). As far as K^+ is concerned, it is involved in the opening and closing of stomata. By affecting K^+ influx, B was also found involving in enhancement of stomatal opening in epidermal strips of dayflower (*Commelina communis*) (41). A number of researchers have observed the excessive leakage of K^+ with B deficiency that leads to a decrease in membrane integrity. Some researchers consider this effect of B as a primary effect while others attribute it to secondary effect of boron deficiency.

Uptake rate of phosphate is decreased by B deficiency and is rapidly restored by resupply of B to deficient plants for one hour (40). More rapid effects of B on ion influx or efflux were shown by Poole (32) in *Zea mays* (maize). He found that resupply of B to deficient maize for one hour caused a significant restoration of phosphate uptake (Table 1).

The data (Table 1) show the variation in phosphorus uptake (nmol/g/h) in faba bean and maize under the pretreatment of root tips with B for one hour and without pretreatment (no B) of root tips. The data markedly indicate that pretreatment of root tips increased the uptake of inorganic phosphorus both in faba bean and maize as compared to without pretreatment.

Table 1. Effect of treatment on subsequent uptake of inorganic phosphate by root tip zones of faba bean *(Vicia faba)* and maize (*Zea mays*) grown in (+ B) or (- B)

Pretreatment of root tips	Phosphate uptake (nmol/g/h)			
	Faba bean		Maize	
	+ B	- B	+ B	- B
No boron	112	52	116	66
10^{-5} M B	152	108	190	171

Source: Poole (32)

Phenol metabolism

Phenol metabolism also plays a very important role in plant growth which seems to be affected by B nutrition. Kamali and Childers (24) studied the effects of B deficiency on several phenolics and enzyme activities involved in the biosynthesis of these compounds in tobacco plant. In B-deficient plants a higher amount of phenolic compounds is accumulated (10). This higher amount of phenolic is very hazardous for plants. With increase in the amount of phenolic compounds, enzymatic or non-enzymatic oxidation takes place, in which phenolic compounds act as substrate. Thus, toxic quinones and destructive O_2 species are generated (1, 23). The phenolics after oxidation corroborate changes in ion fluxes accompanied by changes in membrane potential (19). It has been suggested that phenolics result in reversible alterations in membrane permeability, and this effect of phenolics occurs during their passage through the membranes (18, 19).

In B-deficient plants, not only the phenolic compounds increase but also defence capacity of cells against toxic O_2 species is weakened due to reduced levels of ascorbic acid, SH-compounds and H_2O_2 scavenging enzymes (9). So, it can be suggested that B deficiency renders membrane leakiness and alteration in ion flux characterized by peroxidative damage and structural alteration in plasma membranes.

Boron and nitrogen fixation

Boron is also involved in nitrogen fixation. Loomis and Durst (26) reported that boron is an essential micronutrient required for growth and development of vascular plants, diatoms and species of marine algal flagellates, while bacteria, fungi, green algae and animals apparently do not require B. Not only the leguminous plants but also cyanobacteria require B when dependent on N_2 fixation. Under B-deficient conditions, nodule weight and N_2 fixation capacity of legumes is usually decreased. Bolanos *et al.* (6) investigated the effect of boron on symbiotic nitrogen fixation in pea (*Pisum sativum)*. The absence of boron in culture medium resulted in lower number of nodules and alterations in nodule development. Nodules were not only found less in number but also nodule structure was disorganized and not easily distinguishable in B deficient media. Examination of boron deficient nodules showed dramatic changes in cell wall and in both peribacteriod and infection thread membranes, suggesting a role of boron in the stability of these structures (7). The formations of ineffective nodules have also been reported earlier (8, 42). This alteration of nodule development led to an inhibition of nitrogenase activity. These results indicated that boron is a requirement for normal nodule development and functionality.

Boron and plant reproductive growth

It has been reported that boron deficiency limits reproductive growth. In wheat, B deficiency causes poor anther and pollen development; low grain set and stunted growth (12, 33). *In vitro* germination tests also showed that B was required for pollen germination and tube growth in wheat (12). Seed setting is important for improving yield from any soil particularly salt affected soils. Aslam *et al.* (2) reported better pollination, seed setting, low spike sterility and more grain formation in different cultivars of rice as an effect of boron nutrition. Rashid *et al.* (33) observed a substantial increase in grain yield of rice cultivars, due to reduced panicle sterility after B application. Jiang and Miles (22) identified critical stages of anther development of wheat during which B deficiency caused a significant and irreversible decrease of floret fertility. According to Cakmak (9), B has limited phloem mobility in crops like wheat. Hence, B supply is required for healthy reproductive growth (anther, pollen and ovule development). Loomis and Durst (25) reported the abortion of apical meristems leading to the lack of flowering and development in peach (*Prunus persica*) in boron free medium. Some physiologists (4, 35, 36, 47) have observed the effect of boron nutrition on flowering, stamens, pistil and young reproductive leaves (Table 2 and 3). Generally, the concentration of boron in flower, stamen, and pistil is increased with increase in boron supply from low to adequate level. This is the indicator of response of young reproductive plant parts and leaves to supply of boron.

Table 2. Boron concentration (mg/g dry weight) in young reproductive parts and leaves in oilseed rape (*Brassica napus*), wheat (*Triticum aestivum*) and green gram (*Vigna radiata*) in relation to B supply.

Crops	B supply	Flower	Stamen	Pistil	Leaf
Oilseed rape[1]	Low	-	19	19	10
	Adequate	-	38	40	17
Green gram[2]	Low	30	-	19 [3]	11
	Adequate	61	-	-	34
Wheat [4]	Adequate	-	16[5]	8	3

Adapted from Dell and Huang (14), [1]Pot study in soil by Zhang *et al.* (47) [2] Pot study in solution culture by Bell *et al.* (4). The data for the low boron plants is after transfer to solution without B for 4 days. [3] Data for young pods. [4] Field study by Rerkasem (37). [5] Data for anthers.

Table 3. Mean B concentration (mg/kg) in young whole leaves as affected by B application to a B-deficient media in wheat (*Triticum aestivum* L.) and rice *(Oryza sativa* L.*)* cultivars.

B concentration (mg/kg) in leaves

Wheat cultivars	Control	+B	Rice cultivars	Control	+B
Rohtas-90	5.2	11.0	Super Basmati	7.58	11.24
Sindh-81	9.0	17.0	Basmati-6129	9.36	16.19
Faisalabad-85	8.0	10.3	DR-83	9.07	14.70
Rawal-87	9.3	18.0	KS-282	9.86	16.67
Pak-81	8.7	15.8	Basmati-385	7.14	8.42
Sariab-92	10.0	19.5	Pakhal	9.29	11.56
Inqalab-91	7.2	20.7	Basmati-370	7.43	9.79
Bakhtawar	11.0	21.0	IR-6	8.62	11.31

Adapted from Rashid *et al.* (35)

SUMMARY

Above review indicates that boron performs many functions in cell walls (30) and cellular activities (11). Boron deficiency renders decrease in cell wall plasticity (21) leading to failure of newly divided cells to enlarge (15). As far as plasma membrane is concerned, adequate level of boron stops the accumulation of phenolics and ceases the oxidation of components of plasma membranes. Further it is also involved in the generation of H^+ ATPase, which is a driving force for ion uptake. Hence, integrity and functionality of plasma membranes is ensured with adequate supply of boron. The nitrogen fixation ultimately correlates with nitrogenase activity. Oxygen sensitivity of nitrogenase is well known and relates to toxicity of O_2 species such as O_2^- and H_2O_2 (13). Therefore, activity of O_2^- and H_2O_2 scavenging enzymes may play an essential role in protecting nitrogenase against toxic O_2 species. Since nitrogenase activity is dependent on the development of effective nodules, any alteration in nodule development inhibits the nitrogenase activity. Boron accelerates nitrogenase activity through effective nodule development for nitrogen fixation. Plants reproductive growth is ceased with the deficiency of boron. This retarding growth is considered due to the low phloem mobility of boron. In brief, the formation of B complexes with the constituents of cell wall and plasma membrane as well as with the phenolic compounds is a major reason to affect the physiological functions of boron.

Pollard *et al.* (31) reported several impairments as a result of B deficiency, such as sugar transport, cell wall synthesis, signification, cell wall structure, carbohydrate metabolism, RNA metabolism; respiration, indole acetic acid (IAA) metabolism, phenol metabolism, and membrane integrity.

The above discussion reveals unique physiological role played by boron in plants. However, despite such numerous effects of B, no evidence has yet been presented that B is an enzyme constituent or it has a direct role in enzyme activities. It is also not clear whether above mentioned changes are precursor of direct functions of B or the changes are of an indirect nature.

Therefore, a lot of research activities are required to have an insight whether role played by boron nutrition is primary or secondary.

REFERENCES

1. Appel, H.M. 1993. Phenolics in ecological interaction: the importance of oxidation. J. Chem. Ecol. 19: 1521–1552.
2. Aslam, M.I., H. Mahmood, R.H. Qureshi, S. Nawaz and J. Akhtar. 2002. Salinity tolerance of rice as affected by boron nutrition. Pak. J. Soil Sci. 21: 110-118.
3. Barr, R., M. Bottger and F.L. Crane. 1993. The effect of B on plasma membrane electron transport and associated proton secretion by cultured carrot cells. Biochem. Mol. Biol. Int. 31, 31-39.
4. Bell, R.W., L. McLay, D. Plaskett, B. Dell and J.F. Loneragan. 1990. Internal boron requirements of green gram (*Vigna radiata*). *In:* Plant Nutri. Physiol. Appli. M.L van Beusichem (ed.). Kluwer Academic Publishers, Dordrecht, the Netherlands. p. 275-280.
5. Blaser-Grill, J., D. Knoppik, A. Amberger and H. Goldbach. 1989. Influence of boron on the membrane potential in *Elodea densa* and *Helianthus annus* roots and H^+ extrusion of suspension cultured *Daucus carota* cells. J. Pl. Physiol. 90: 280–284.
6. Bolanos, L., E. Esteban, C. De Lorenzo, M. Fernandez-Pascual, M.R. De Felipe, A. Garate and I. Bonilla. 1994. Essentiality of boron for symbiotic dinitrogen fixation in pea (*Pisum sativum*) rhizobium nodules. Pl. Physiol. 104: 85–90.
7. Brenchley, W.E., and H.G. Thornton. 1925. The relation between the development, structure and functioning of the nodules on *Vicia juba,* as influenced by the presence or absence of boron in the nutrient medium. Proc R SOC Lond. Biol. Sci. 498: 373-398.
8. Brown, P.H., and B.J. Shelp. 1997. Boron mobility in plants. Pl. Soil. 193:85-102.
9. Cakmak, I. 1994. Activity of ascorbate-dependent H_2O_2-scavenging enzymes and leaf chlorosis are enhanced in magnesium- and potassium-deficient leaves, but not in phosphorus-deficient leaves. J. Exp. Bot. 45:1259–1266.
10. Cakmak, I. and V. Romheld. 1997. Boron deficiency induced impairments of cellular functions in plants. Pl. Soil. 193:71-84
11. Cheng, C. and B. Rerkasem. 1993. Effects of boron on pollen viability in wheat. Pl. Soil. 155/156:313-315.
12. Dalton, D. A, S. A. Russell, F. J. Hanus, G. A. Pascoe and H .J. Evans. 1986. Enzymatic reactions of ascorbate and glutathione that prevent

peroxide damage in soybean root nodules. Proc. Nat. Acad. Sci. USA .83:3811–3815.

13. Darvil, A., M. McNeil, M. P. Albersheim and D. P. Delmer. 1980. The primary cell wall of flowering plants. *In*: The Biochemistry of Plants. A comprehensive treatise. Tolbert, N.E (ed.). Pp. 91-161. Academic Press, New York.
14. Dell, B. and L. Huang. 1997. Physiological response of plants to low boron. Pl. Soil. 193: 103-120.
15. Fleischer, A., C. Titel and R. Ehwald. 1998. The boron requirement and cell wall properties of growing and stationary suspension-cultured *Chenopodium album* L. cells. J. Pl. Physiol. 117:1401-1410.
16. Glass, A.D.M. 1973. Influence of phenolic acids on ion uptake. I. Inhibition of phosphorus uptake. Pl. Physiol. 51: 1037–1041.
17. Glass, A.D.M. 1974. Influence of phenolic acids upon ion uptake. III. Inhibition of potassium absorption. J. Exp. Bot. 25: 1104–1113.
18. Glass, A.D and M. Dunlop. 1974. Influence of phenolic acids on ion uptake. IV. Depolarisation of membrane potentials. Pl. Physiol.54: 855–858.
19. Goldbach, H.E., D. Hartmann and T. Rotzer. 1990. Boron is required for the ferricyanide-induced proton release by auxins in suspension cultured cells of *Daucus carota* and *Lycopersicon esculentum.* Physiol. Pl. 80:114–118.
20. Hu, H. and P.H. Brown. 1994. Localisation of boron in the cell wall and its association with pectin. Evidence of a structural role of boron in the cell wall. Pl. Physiol. 105:681–689.
21. Huang, L., J. Pant, B. Dell and R. Bell. 2000. Effects of boron deficiency on anther development and floret sterility in wheat (*Triticum aestivum* L. 'Wilgoyne'). Ann. Bot. 85:493-500.
22. Jiang, Y and P.W. Miles. 1993. Generation of H_2O_2 during enzymic oxidation of catechin. Phytochem. 33: 29–34.
23. Juan, J., Camacho-Cristóbal, D. Anzellotti and A. González-Fontes. 2002. Changes in phenolic metabolism of tobacco plants during short-term boron deficiency. J. Pl. Physiol. Biochem. 40:997-1002.
24. Kamali, A. R. and N. F. Childers. 1970. Growth and fruiting of peach in sand culture as affected by boron and fritted form of trace elements. J. Amer. Soc. Hort. Sci. 95:652-656.
25. Loomis, W.D. and R.W. Durst. 1991. Boron and cell walls. Curr. Topics Pl. Biochem. Physiol. 10:149–178.
26. Loomis, W.D and R.W. Durst. 1992. Chemistry and biology of boron. Bio Factors. 4:229–239.
27. Marschner, H. 1995. Mineral Nutrition of Higher Plants. p. 379 - 396. Academic Press, San Diego, USA.

28. Martin, F. and M. Theiller. 1993. Boron distribution in parenchyma cells of clover leaves. Pl. Physiol. Biochem. 31:777-786.
29. Matoh, T., S. Kawaguchi and M. Kobayashi. 1996. Ubiquity of a borate-rhamnoglacturonan II complex in the cell walls of higher plants. Pl. Cell Physiol. 37:636-640.
30. Parr, A.J. and B.C. Loughman. 1983. Boron and membrane function in plants. *In:* Metals and Micronutrients, Uptake and Utilisation by Plants. Robb, D.A and W.S. Pierpoint (eds.). Academic Press, New York. p. 87–107.
31. Pollard, A.S., A.J. Parr and B.C. Loughman. 1977. Boron in relation to membrane function in higher plants. J. Exp. Bot. 28:831–841.
32. Poole, R.J. 1978. Energy coupling for membrane transport. Ann. Rev. Pl. Physiol. 29:437-460.
33. Rashid, A., E. Rafique and N. Bughio. 1994. Diagnosing boron deficiency in rapeseed and mustard by plant analysis and soil testing. Communications in Soil Science and Plant Analysis. 25(17/18):2883-2897.
34. Rashid, A., M. Yasin, M. Ashraf and R.A. Mann. 2004. Boron deficiency in calcareous soil reduces rice yield and impairs grain quality. International Rice Research Notes. 29: 58-60.
35. Rashid, A., S. Muhammad and E. Rafique. 2005. Rice and wheat genotypic variation in boron use efficiency. Soil Environ. 24:98-102.
36. Raven, J.A. 1980. Short and long distance transport of boric acid in plants. New Phytol. 84: 231-249.
37. Rerkasem, B. 1996. Boron and plant reproductive development. *In:* Sterility in Wheat in Sub-tropical Asia: Extent, Causes and Solutions. Rawson, H .M. and K. D. Subedi (eds.). p. 32-35. ACIAR Proc. No. 72.
38. Robertson, G.A. and B.C. Loughman. 1973. Rubidium uptake and boron deficiency in *Vicia faba*. J. Exp. Bot. 24:1046–1052.
39. Robertson, G.A., and B.C. Loughman. 1974. Reversible effects of boron on the absorption and incorporation of phosphate in *Vicia faba.* New Phytol. 73:291–298.
40. Roth-Bejerano, N. and C. Itai. 1981. Effect of boron on stomatal opening in epidermis strips of *Commelina communis*. Physiol. Pl. 52:302–304.
41. Schon, M.K, A. Novacky and D.G. Blevins. 1990. Boron induces hyperpolarisation of sunflower root cell membranes and increases membrane permeability to K^+. J. Pl. Physiol. 93:566–577.
42. Serrano, R. 1989. Structure and function of plasma membrane ATPase. Ann. Rev. Pl. Physiol. 40:61-94.
43. Shelp, B.J. 1993. Physiology and biochemistry of boron in plants. *In:* Boron and its Role in Crop Protection. Gupta, U. C. (ed.). p. 53–85. CRC Press, Boca Raton, FL, USA.

44. Sommer, A.L. and H. Sorokin. 1928. Effects of the absence of boron and of some other essential elements on the cell and tissue structure of the root tips of *Pisum sativum.* Pl. Physiol.3: 237-260.
45. Trefil, J.S. 2001. Encyclopedia of Science and Technology; Taylor and Francis Group, New York.
46. Warington, K. 1923. The effect of boric acid and borax on the broad bean and certain other plants. Ann. Bot. 37:629–672.
47. Zhang, X., Z. Shen and K. Shen. 1994. The effect of boron on the development of floral organs and seed yield of rape (In Chinese). Acta Pedologica Sinica. 31:146-151.